Summary.—As evidence for the chemical differentiation of the central nervous system in invertebrates, it has been shown that, in the cephalopod (Loligo pealii), caffein brings about hyperirritability of the cerebral ganglia, while camphor affects the stellar ganglia alone in the same sense. Atropin causes spasms in the squid, but inhibits the activity of the chromatophores.

Camphor shows a selective action on the central nervous system of the shrimp (Crangon vulgaris) paralyzing the elements which function in backward swimming movements and exciting those controlling forward movement.

Atropin increased the sensitivity of all the forms tested.

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[2] Moore, A. R., *Science, New York*, N. S., **38**, 1913, (131–133).

PROOF OF THE MUSCLE TENSION THEORY OF HELIOTROPISM

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That the mechanism by which heliotropic organisms are oriented to light should be identical with that for the orientation to the galvanic current was demanded by the tropism theory developed by Loeb in 1888.[1] The identity of the mechanism in sessile forms was early established by Loeb, while more recently Bancroft[2] has clearly shown that the tenets of the theory hold also in the movements of *Euglena*, which are accomplished in an identical way whether under the influence of light or of the constant current.

It is the aim of this paper to show that the movements of many heliotropic insects under the influence of light are to be explained as forced motions due to the effects of light upon the tension or tonus of the muscles and that in this regard, there exists an exact analogy to the effects of the constant current in the animals investigated.

Loeb and Maxwell[3] showed that when a constant current passed from side to side of *Palæmonetes* the legs on the anodal side were flexed, while those on the cathodal side were extended. With the anode at the anterior end the anterior legs were flexed and the posterior extended. Reversal of the current reversed the condition of tension in these legs and body changes were also induced. The whole response persisted while the current flowed and put the animals in such a condition that any movement forced them toward the anode. Similarly it was shown

by Loeb and Garrey[4] that *Amblystoma* larvae reacted to the constant current in such a way that the muscle tonus was different depending upon the direction of the current. With the anode at the anterior end, the body curved ventrally and the legs were directed backward, while with the cathode at the head end the body was in the opisthotonic condition, concave dorsally, and the legs were directed forward. These differences in muscle tension made motion difficult or impossible in any direction except to the anode, toward which the animals were forced to move.

In the heliotropic insects the characteristic reactions are mediated through the eyes, the central nervous system, and thus reflexly, the musculature. Loeb proposed the following theory of the direction of the motions of such heliotropic animals.[5] The "photosensitive elements are arranged symmetrically in the body and through nerves are connected with symmetrical groups of muscles. Light causes chemical changes in the eyes. . . . . If the rate of photochemical reaction is equal in both eyes the effect upon symmetrical muscles is equal, and the muscles of both sides of the body work with equal energy. If a positively heliotropic animal is struck by light from one side, the effect on the tension or energy production of muscles connected with this eye will be such that an automatic turning of the head and the whole animal toward the source of light takes place," until the eyes are equally illuminated, when the symmetrical muscles work equally so that the animal will continue to move in this direction, or any deviation from this line of orientation will result in a repetition of the manouver.

It is our purpose to show that inequality in the illumination of the two eyes of many insects does in reality produce the differences in muscular tension demanded by this theory, that their movements are determined by this condition, that the phenomena are quite general in this group of animals and identical with those described for galvanotropism where the tension theory is proven.

Holmes[6] showed that the tonus of the muscles of the water scorpion, *Ranatra*, was markedly affected by illuminating the animal from different directions and by blackening different parts of the eyes, thus changing the equality and symmetry of illumination of the two sides. His results were in absolute harmony with Loeb's theory, the animals reacted according to its demands with 'machine-like' precision. The striking similarity to the behavior of *Palæmonetes* or *Amblystoma* when under the influence of the galvanic current would have sufficed to establish the identity of heliotropism with galvanotropism, had it not been for the diverting effect of Holmes's psychological speculation,

centering as it did upon other features in the behavior of *Ranatra*. This case stands as an isolated example whereas, the features it presents are in reality generally applicable to heliotropic animals, since our experiments have demonstrated their existence in practically every group of the insecta. They are well shown by many genera of butterflies and moths, by the bees, by many of the commoner flies including *Musca*, *Caliphora*, *Tabanus*, and *Eristalis*. While future reference will be made to these forms, the present communication will deal mainly with the reactions of the robber flies, in some forms of which the effects of light on the muscle tonus are most striking. The best of these which has come to our notice is one of the large brown forms, *Proctacanthus*, although *Promachus* and *Deromyia* show the reactions well.

Methods were used to produce unequal illumination, usually by blackening some part of the eyes with asphalt black, which is practically opaque and hardens into a brittle shell-like film upon drying.

1. Blackening all of one eye. When one eye of positively heliotropic insects is blackened, circus motions are made toward the opposite (normal) side and in all the forms studied they occur both when flying and creeping, as noted by Parker for *Vanessa antiopa*.[7] They may be noted in practically all of the commoner butterflies. Differences in the tonus of the muscles of the two sides are in evidence when the animals are at rest under constant illumination. The bodies are tilted well toward the side of the good eye and the legs of that side are flexed with the body resting against their upper segments, while the terminal segments of that side are well under the body, and those of the opposite side are extended away from the body. The head is usually rotated on the body so that both antennae may actually be below the line of the wings.

The robber fly, *Proctacanthus* (Sp. ?) shows the tonus changes of the legs much more strikingly than any other insect examined. On the side of the good eye they show a continued state of flexion involving all three legs. The anterior leg may be so far adducted as to cross under the body farther to the side of the blackened eye than the corresponding leg of that side. The legs on the side of the blackened eye are more extended than normally and spread farther apart. The body may tilt so far toward the side of the normal eye as to press the legs to the table. The head not only rotates on the long axis of the body toward the good eye but is also flexed toward that side, a considerable angle appearing between the head and thorax. In some cases the abdomen also shows flexion concavely toward the side of the good eye even when the animal is at rest. The posture assumed is the characteristic one assumed by

Palæmonetes when the constant current is passed through the body from side to side, and by *Ranatra* when illuminated from one side. The figures of the authors referred to above in this connection will serve for illustration of the conditions resulting from our experiments.

All of the muscular conditions upon which the resting postures are dependent are accentuated by activity. The robber flies move in circles by farther flexing the legs on the side of the functioning eye and extending those on the side of the blackened eye. The head bends farther toward the center of the circle and the abdomen curves so that the body is concave, forming an arc of the circle in which movement is executed.

2. *Illuminating one eye.* Bringing one eye of *Proctacanthus* into the bright beam of light directed through the objective of the optical system of the string galvanometer, while the other eye is illuminated only by the subdued light of the optical room, promptly produced the same postural relations described in the previous section. In this case the diffusely illuminated eye corresponds to the blackened eye. The result is due simply to a difference in the intensity of illumination of the two eyes. Mast[8] has produced similar tonus differences by reflecting light from a small mirror on one of the eye spots of *Arenicola* larvae; the body musculature contracted on the brightly illuminated side. This observation we have repeated and noted further that the contracted state persists as long as the light is held on the eye spot. The same curvatures have been noted by us when the constant current is passed transversely through the body of the marine worm *Podarke* and have also been described by Moore and Kellogg for the earthworm.[9] The general mechanism is the same for the action of light and the galvanic current.

3. *Blackening the lower half of both eyes equally* results in a symmetrical position of the legs of the two sides but the anterior and middle pair are extended forward to the maximal extent, producing a striking posture in which the anterior end of the robber fly is pushed up and back from the surface of the table. The front pair of legs may even be poised up in the air. The body is in opisthotonus with the abdomen concave on the dorsal side, while the head is tilted far up and back on the long axis of the body. The whole posture is that assumed by *Amblystoma* or by *Palæmonetes* as described above, when subjected to the influence of the constant current with the cathode at the anterior end. Holmes showed similar postures for *Ranatra* with a light placed above and posterior to the animal.

When walking these robber flies gave the impression of trying to climb up into the air. The wings are frequently somewhat spread and the

animal may push itself up and back until poised vertically on the tips of the wings and abdomen. The tendency to fly is very pronounced in this condition and upon the slightest disturbance the fly soars upward and backward, striking the top of a confining glass dish or completing a circle by "looping the loop" backward. If it falls upon its back it rights itself by turning a backward somersault. Unequal blackening of the lower parts of the two eyes results in a combination of the effects just described, with those described for blackening one eye, for the animal also performs circus motions.

4. *With the upper halves of the eyes blackened* the attitude is the reverse of that described in the preceding section. The anterior and middle pairs of legs are flexed. The anterior and posterior ends of the body bend ventrally with the body in emprosthotonus. The head is bent far down until its anterior aspect is parallel to the surface of the table. The animal may actually stand on its head, but the abdomen retains its ventral curvature, leaving a considerable angle open between its dorsum and the wings which normally rest on it.

In both walking and flying it continually keeps close to the table, and upon encountering an obstacle it frequently does a forward somersault. If it gets on its back it rights itself with greatest difficulty as its efforts simply result in bending the tail and head ventrally until they may form a complete ring. In galvanotropism the same general picture is presented by *Palæmonetes* and *Amblystoma* when the anode is at the head end, the tonus changes involved being identical in the two conditions.

5. *By blackening the upper half of one eye and the lower half of the other*, circus motions are performed toward the side with the lower half blackened. If for example the lower half of the right eye and the upper half of the left eye of the robber fly are blackened flexion of the anterior leg on the right side results. There is extension of the anterior leg on the left side. The body is thus somewhat twisted on its long axis for there is also flexion of the posterior leg on the left side and extension of its mate on the right side. Such a bizarre effect is hardly explicable by any reçourse to the assumption that the animal is "avoiding the darkened field." In reality the tilting of the body and the twist of the head are toward the blackened part of the eye viz., *down* on the side on which the lower half of the eye is blackened, and *up* on the side on which the upper half has been blackened. The result is readily explained on the basis of a crossed innervation from the eyes to the extensor muscles of the opposite side, a view for which much evidence is at hand.

6. *Blackening corresponding halves of both eyes of Proctacanthus*, for example, the outer half of the right eye and the inner half of the left eye, causes postural changes similar to those produced by blackening all of one eye (the right) and circus motions away from the side to which the black has been applied, i.e., to the left in our example. This statement of fact is, however, capable of overemphasis for the intensity of the reaction depends upon the relative amount of black applied to each eye, thus if a greater area of the inner side of the left eye be blackened or a lesser area on the outer (right) side of the right eye the tendency to move in a circle to the left is lessened, nullified, or even reversed by combining the two procedures. This fact is an interesting and fatal contradiction to the view that the postures are assumed, and the circus motions made, in an attempt "to avoid the dark field which appears as an obstruction to the path." The reaction is a quantitative one and depends on the relative areas blackened as much as upon the part of the eye covered. The space relation of light fields to dark fields, does not change in the above experiment but the tonus of the muscles does change with the change in the areas blackened, whereby the behavior of the robber fly is reversed and it circles toward the side on which both eyes have been blackened.

When either the inner halves or the outer halves of both eyes are blackened, the muscles of the two sides remain absolutely symmetrical provided the eyes are equally and symmetrically painted. If the painted area is considerably less on one eye than on the other, the tonus changes again approach those found by blackening all of one eye and the animal, in walking, circles to the side with the greater area exposed to the action of light. Complete blackening of both eyes results in marked relaxation of all the musculature, although the two sides are symmetrical.

7. All the experiments show that the muscle tone is dependent upon the intensity of the light and that the postures assumed depend upon the relative differences in the illumination of the eyes. In animals with one eye completely covered the radii of the circles in which they moved were shorter the more intense the illumination of the normal eye. With one eye partially covered the circles were larger than when completely covered and in the same way, the circles were larger when one eye was covered by a film of collodion or of brown shellac, which admit some light, than when subsequently covered by opaque asphalt black. When one eye was partially covered by central application of the black paint the tilting and circling to the opposite side were abolished or reversed by brilliant illumination of the partially blackened eye. These re-

sults explain why a positively heliotropic animal with one eye blackened approaches a light by a series of alternating small and large circles, the former being executed when the good eye is illuminated from the source of light, the larger when it is in the shadow.

8. Differential sensibility. Robber flies with one eye blackened show the postural conditions in the most pronounced way in the early morning or after being kept for some hours in the dark. Constant exposure to the light produces considerable fatigue of the eye with recovery in the dark. These facts among others suggested the possibility of producing a different sensitiveness of the two eyes and corresponding differences in the muscle tonus with asymmetry of position, and in physiological action of the muscles of the two sides of the body when the two eyes were equally illuminated. Such an experiment constitutes a crucial test of the tonus theory of heliotropism. It succeeded beyond our greatest expectations. Asphalt black was applied to the right eye of several specimens of *Proctacanthus.* In two or three days the paint had formed a brittle shell. During this time the blackened eye had become 'dark adapted.' When such a fly is exposed to light, it tilts and circles to the left. If now the brittle shell is cracked off the right eye by carefully pinching with fine forceps, the exposure of this very sensitive eye to light results in a reversal of the whole picture; the fly circles toward the side from which the black was removed. Although the illumination of the two eyes is of equal intensity, what was the normal eye now becomes relatively a darkened eye owing to its lesser sensitiveness. A differential effect results, probably due to a difference in the rate of photochemical change in the two eyes. This reversal of the muscle tonus, and of forced motions, may persist for an hour or two or even longer, until the two eyes become, as they ultimately do, of equal sensitiveness and the fly behaves like a normal animal.

These experiments are not only incompatible with any avoidance idea, for after removal of the black there is nothing to avoid, but they are also incompatible with the conception of 'habit formation,' for "habit" in the performance of the circling movements is of no avail when light is admitted to the darkened eye. The animals circle to that side because the tonus of the muscles is such that they are forced to do so.

9. Post mortem rigor. *Proctacanthi* kept in a moist atmosphere but without animal food, have lived two or three weeks. During this time if one eye was blackened the tonus change in the muscles became almost a fixed condition, probably the result of an atrophy of the muscles or a lack of tonus, similar to the effects of disuse. Death supervening, the

onset of rigor exaggerated the condition existing prior to death and the animal stiffened in the characteristic postures. This follows the rule for rigor mortis, that the more strongly acting muscles contract more strongly after death. This fact lends additional proof for the tonus theory of the tropisms.

Conclusion.—These experiments remove, in our opinion, the last doubt that the motions of animals to or from a source of light are due to an influence of the light on the tension of muscles of different sides of the body whereby the animal is automatically carried to or from a source of light.

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[4] Loeb, J., and Garrey, W. E., *Ibid.*, **65**, 1896, (41).

[5] Loeb, J., *The Organism as a Whole*, New York, 1916, pp. 257–259.

[6] Holmes, S. J., *J. Comp. Neur. and Psychol., Wistar Inst., Philadelphia*, **15**, 1905, (305).

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CHANGEABLE COLORATION IN BRACHYURA

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Although changes in coloration have been observed commonly in crustacea, only two recorded cases appear to refer to Brachyura. Fritz Müller reported to Darwin[1] that the male of a Brazilian species of *Gelasimus* is subject to rapid and remarkable changes in appearance. R. P. Cowles[2] has also described changes in color in *Ocypoda arenaria* Say, which he believes are in the main, if not entirely, dependent upon changes in the intensity of the light and variations in the temperature to which the creatures are exposed. It would seem, however, that crabs are able at least to change their shade much more commonly than recorded observations would indicate and that other factors than those suggested may determine their coloration at a given moment.

Portunus depressifrons Stimp., *Callinectes ornatus* Ord. and *C. marginatus* A. M.-Edw. display striking changes in coloration under certain conditions. Others less obvious or less closely studied have been noted too in *Portunus spinicarpus* Stimp. and *P. sayi* Gibbes and in